

## ECOLOGICAL CONSEQUENCES OF AGONISTIC INTERACTIONS IN LIZARDS

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**Abstract.** It is relatively easy to document direct agonistic interactions among or within species that lead to exclusion of subordinate animals from preferred habitats. It is more difficult to measure the competitive effects of that exclusion on the “loser.” Thus, much behavioral research assumes that the intensity of agonistic interactions is correlated with their cost to performance, but does not directly measure such a cost. We examined fitness-associated traits of pregnant viviparous scincid lizards (*Eulamprus heatwolei*) in outdoor enclosures under three conditions: alone, with a conspecific, or with a larger and more aggressive heterospecific (*Egernia saxatilis*, a sympatric scincid species). As in previous laboratory studies, *Egernia saxatilis* attacked *Eulamprus heatwolei* and excluded individuals of the smaller species from warmer shelter sites. However, *Eulamprus heatwolei* were able to maintain “normal” schedules of body temperatures and food intake, apparently by modifying their behavior to minimize encounters with their aggressive cage mates. Accordingly, the subordinate animals showed no overt ill effects in spite of strong agonistic interactions: the body condition, locomotor performance, and corticosterone levels of subordinate *Eulamprus* housed with *Egernia* were indistinguishable from those of lizards kept in solitary cages or with conspecifics only. Similarly, the offspring of these pregnant females were born at the same time, and with similar phenotypic traits, as the offspring of control females. Thus, even in situations of intense interspecific aggression and consequent habitat exclusion, behavioral flexibility of the subordinate animals may decrease or eliminate the inferred ecological consequences of that interaction.

**Key words:** aggression; agonistic behavior; behavioral flexibility; habitat exclusion; *Egernia saxatilis*; *Eulamprus heatwolei*; intraspecific; interspecific; scincid lizards; shelter; shelter sites; skink.

### INTRODUCTION

Individuals interact in a myriad of ways with both conspecifics and heterospecifics (Knox et al. 1994, Begon et al. 1996). There are many clear examples where-by interactions between animals (both of the same species and different species) influence biologically significant behaviors such as habitat use, feeding, and thermoregulation (Petren and Case 1996, Ybarrondo and Heinrich 1996). However, extrapolation of these results to the biological consequences of such interactions remains a major challenge. Behavioral scientists have widely presumed that subordinate animals exposed to strong agonistic interactions will exhibit reduced performance, thus forging a link between agonistic dominance and ecological consequences (Greer 1989, Krebs and Davies 1997). Nonetheless, evidence for such a link is generally weak or indirect. Even if two organisms engage in vigorous agonistic interactions during staged encounters, a complex environment may allow them to modify their behavior in ways that reduce the ecological impact of such interactions. Thus,

the competitive effect of these interactions may be lower than might have been inferred at first sight.

Many of the best examples of the ecological effects of interspecific interactions come from studies of introduced species, or of native taxa that are expanding their ranges into anthropogenically modified habitats (Williamson 1996, Mack et al. 2000). Such effects include exclusion of species or partitioning of resources (Diamond 1978). Even when species do coexist, agonistic interactions may result in reduced abundance, fecundity, growth, or survival (Case et al. 1994, Eccard and Ylonen 2002, Wauters et al. 2002).

The proximate mechanisms by which agonistic interactions may reduce organismal fitness undoubtedly are complex, ranging from direct injury inflicted by aggressive heterospecifics through to more subtle pathways such as reduced food intake or transfer of disease organisms (Ducey et al. 1994, Hudson and Greenman 1998, Gaymer et al. 2002). One of the most important such pathways may be via habitat use, whereby one taxon excludes another from preferred shelter and foraging sites (Nakata and Goshima 2003, Ovadia and zu Dohna 2003). In turn, exclusion from preferred sites potentially can have numerous consequences for the excluded organisms. Suboptimal moisture conditions can result in dehydration (Jaeger 1971), and thermally

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suboptimal habitats can have major physiological consequences for ectotherms (Huey et al. 1989). Overt signs of such competitive impacts might include decreased survival probabilities, growth rates, body condition, or reproductive output (Rome et al. 1992). On a physiological level, individuals of the subordinate taxon may exhibit elevated levels of the stress hormone corticosterone (Wingfield et al. 1991, Creel 2001). High levels of stress hormones can influence not only the phenotypic traits of the individual directly concerned, but also its offspring: prenatal stress can negatively affect offspring birth mass, growth, behavior, survival, and response to stressors (Meylan et al. 2002, Rondo et al. 2003, Hayward and Wingfield 2004).

Thus, extensive research has confirmed that interspecific agonistic interactions can be intense. However, extrapolating this result to the fitness consequences of such interactions is difficult, because of the possibility that sympatric taxa will evolve strategies to minimize the costs of these agonistic interactions. For example, even a minor change in activity times or places might greatly reduce the vulnerability of a subordinate taxon to harassment by a dominant species (Morrison 2000, Munday et al. 2001). In support of this hypothesis, it is striking that the best field evidence for intense ecological "costs" comes from studies on invasive taxa rather than equilibrium communities (Williamson 1996, Mack et al. 2000). If it is true that the intensity of competitive effects is reduced by coevolution among sympatric taxa, then extrapolations from observations of intense agonistic interactions may provide a misleading basis for inferences about the ecological consequences of such interactions. We set out to test this hypothesis by studying the effects of aggression between lizard species that naturally co-occur in high-elevation (cool-climate) locations in southeastern Australia.

To understand whether or not agonistic interactions actually translate to ecological costs, we need a system in which species experience intense aggression, and we can readily identify (and thus manipulate) the resource being contested. Then, we can quantify the effects of aggression on resource use and on fitness-related attributes of the subordinate organism. Viviparous scincid lizards in the Kanangra-Boyd wilderness of southeastern Australia provide such a system. Several species are broadly sympatric; all center their activities on one or a few vigorously defended shelter sites (generally, rock crevices); all taxa prefer warmer (sun-exposed) shelters, which are limited in this relatively cold area, so that the selected shelter-site attributes overlap strongly among taxa; and both laboratory and field observations reveal frequent, intense physical battles, both among and within species, for possession of optimal shelter sites (Langkilde et al. 2003, Langkilde and Shine 2004).

Do these interspecific contests for shelter sites have significant ecological consequences for the losers of

such battles? In such a system, we can predict that subordinate lizards excluded from the warmer (preferred) sites would thereby experience lower body temperatures, in turn reducing rates of feeding, digestion, and growth; thus, we expect to see reduced body condition in such animals. Additionally, stress (and, thus, corticosterone levels in the blood) is likely to be higher as a result of exclusion from preferred sites. Lastly, the effects of aggression are likely to be even greater if the focal animals are pregnant. In viviparous reptiles, maternal body temperatures and stress both can influence the phenotypic traits (and thus viability) of the offspring by modifying embryonic development during pregnancy (Arnold and Peterson 2002, Wapstra et al. 2004). Thus, we may expect to see significant ecological effects of exclusion from shelter sites not only on the pregnant lizards themselves, but also on their offspring. Alternately, these species may have evolved strategies to reduce the costs associated with intense interspecific aggression. This broad suite of predictions for an array of traits means that the Kanangra-Boyd lizard assemblage provides a robust opportunity to examine the degree to which interspecific conflict over shelter sites translates into ecological "costs" for subordinate animals and their offspring.

## METHODS

### *Study species*

Five species of scincid lizards are abundant in Kanangra-Boyd National Park (33°58.270' S, 150°03.346' E), 160 km west of Sydney, New South Wales, Australia. This high-elevation (1200 m a.s.l.), mountainous region is covered by eucalyptus forest interspersed with large rock outcrops. All five species are insectivorous and are widely distributed through montane areas of southeastern Australia. All are viviparous, and females give birth to one litter per year, in late summer (Greer 1989). These diurnally active heliotherms focus much of their activity around one or a few permanent shelter sites (crevices in rocks or logs; Greer 1989). Quantitative analysis has revealed extensive overlap between the abiotic characteristics of retreat sites used by all five species, all of which select warmer-than-average shelters in relatively open areas (Langkilde et al. 2003). Individuals of all of these species often are found in close proximity (<1 m apart), but we have never found more than a single species inside any given shelter (Langkilde et al. 2003, Langkilde and Shine 2004). This exclusivity is maintained by strong agonistic interactions both between and within species (Langkilde and Shine 2004).

The present study is focused on two of the species in this assemblage: *Eulamprus heatwolei* and *Egernia saxatilis*. We henceforth will refer to these species by their generic names for simplicity. *Egernia* is a relatively large skink (mean adult mass 35.1 g), and these animals frequently attack the smaller *Eulamprus* (mean

adult mass 12.2 g) that attempt to enter a crevice (Langkilde and Shine 2004). In consequence, both field and laboratory data show that *Eulamprus* avoid crevices occupied by *Egernia* (Langkilde and Shine 2004), and rapidly flee from such crevices if they encounter the resident lizard (T. Langkilde and R. Shine, unpublished data).

#### Enclosure trials

**Experimental design.**—Our aim was to ask whether aggressive interactions, as seen in the laboratory and the field, have ecological consequences. To do so, we need to manipulate the intensity of interspecific aggression (presence or absence of competing taxa) while standardizing the availability of alternative shelter sites. In practice, we cannot do this in the field. However, it is straightforward to set up outdoor arenas that mimic many of the features of the natural habitat, and this is the approach that we have taken. *Eulamprus* is exposed to both intra- and interspecific aggression over shelter sites (Langkilde and Shine 2004). Our experiment was designed to compare the effects of these two types of aggressive interactions on traits of reproducing female *Eulamprus* and their offspring. To do so, we collected 80 female *Eulamprus* and 20 female *Egernia* from Kanangra-Boyd in November 2003. Sixty female *Eulamprus* were used as focal individuals, and the other lizards were used as stimulus animals. In previous studies, a lizard's sex did not affect its intensity of aggression (Langkilde and Shine 2004). Therefore, we used only females as stimulus animals to reduce any potentially confounding effects. We randomly assigned each of the 60 focal *Eulamprus* to one of three treatments, housing them alone ( $n = 20$ ), with another female *Eulamprus* (intraspecific aggression;  $n = 20$ ), or with a female *Egernia* (interspecific aggression;  $n = 20$ ). Several of the focal *Eulamprus* did not give birth (these animals presumably either were mistakenly classified as gravid, or aborted during the study), and therefore were excluded from analyses of the effects of aggression. Thus, final sample sizes for focal *Eulamprus* in analyses were 15 lizards housed alone, 16 housed with another *Eulamprus*, and 16 housed with an *Egernia*. The *Eulamprus* were always smaller than the *Egernia* with which they were housed (difference in snout-vent length (SVL) is  $24 \pm 3.6$  mm, mean  $\pm$  SE; range 5–38 mm).

**Housing.**—Each focal *Eulamprus* was housed (either singly or with another lizard) in one of 60 large ( $2 \times 2 \times 1$  m, length  $\times$  width  $\times$  depth) seminatural outdoor enclosures. In the field, these species preferentially select rock shelters positioned in open, sunny areas (Langkilde et al. 2003). To replicate this natural variation in sun exposure, one half of each enclosure was covered with shade cloth that excluded 90% of the incoming solar radiation. The walls of the enclosures provided further shading. Each enclosure was furnished with a brick-on-brick shelter positioned in the open,

sunny corner of each enclosure (high-quality shelter), and three shelters (constructed of wood, plastic, and shade cloth) were placed directly onto the sand substrate at the shaded end of the enclosure (low-quality shelters). The brick shelter was consistently warmer than the other shelters and the open sand (brick shelter  $28.75^\circ \pm 0.25^\circ\text{C}$ , other shelters  $20.5^\circ \pm 0.29^\circ\text{C}$ , open sand  $19.9^\circ \pm 0.13^\circ\text{C}$ ; values are means  $\pm$  SE). Lizards were provided water ad libitum, and we provided four crickets per lizard twice weekly.

Focal *Eulamprus* were maintained in these outdoor enclosures for 10 weeks, until shortly prior to parturition (1–24 days prepartum;  $9.9 \pm 0.8$  days, mean  $\pm$  1 SE). They were then moved to the laboratory and individually housed in plastic containers ( $20 \times 12 \times 10$  cm) with a paper substrate, a water dish, and a shelter. The room was maintained at  $16.5^\circ\text{C}$ , with heat for thermoregulation being provided by a strip of heating tape (reaching  $40^\circ\text{C}$ ) running under one end of the container on a 9-h-on : 15-h-off cycle, while the room's overhead fluorescent lights were set on a 12 h on : 12 h off cycle, mimicking field conditions. Water was provided ad libitum and each focal *Eulamprus* was fed four crickets twice weekly. They were given four crickets immediately after giving birth, and again at four days (after the sprint speed trials) and six days post partum.

Upon birth, neonates were individually marked by toe clipping. Sex was determined by hemipene eversion, and males were marked dorsally with a small white spot (Artline 400XF Xylene Free Paint marker, Shachihata, Nishi-ku, Nagoya City, Japan) for easy visual discrimination of sex. Offspring were separated from their mothers and were housed together with their siblings as previously described. Each neonate was fed three small crickets immediately upon transfer, and at four days (during feeding trials) and six days of age.

All stimulus lizards were released at their initial point of capture at the completion of the outdoor enclosure trials, and the focal *Eulamprus* and their offspring were released 7–10 days after parturition.

**Data collection.**—To clarify the effects of aggression on organismal performance of subordinate animals, we measured traits associated with maternal behavior, physiology, and reproductive output, and characteristics of the offspring from these females.

#### Behavior

To see whether or not aggressive interactions with a larger heterospecific lizard affected the behavior of female *Eulamprus*, we quantified their shelter-site use, body temperatures, selected temperatures, food intake, and activity levels. Intra- and interspecific aggression over shelter sites occurs in these species both in the laboratory and in the field (Langkilde and Shine 2004). To ascertain whether similar agonistic interactions occur in outdoor enclosures, we surveyed the enclosures between 09:00 and 10:00 hours, and determined which

individual occupied the warmer (high-quality) shelter site.

Any change in shelter-site use due to aggressive displacement may, in turn, influence the body temperatures achieved by the focal *Eulamprus*. We recorded the body temperatures of 24 focal *Eulamprus* (eight from each treatment) over three days (17–20 December 2003) by gluing thermochron i-buttons (Dallas Semiconductor Corporation, Dallas, Texas, USA) to their dorsal surface. The thermochrons were modified by removing the outer metal shell to reduce their mass (Robert and Thompson 2003), and the small, exposed thermistor was in direct contact with the lizard's dorsal surface when attached. Temperatures obtained using this method correlate highly with the lizards' internal body temperatures (Shine et al. 2003). A thermochron was lost from one focal *Eulamprus* housed with another *Eulamprus*, so this individual was not included in the analyses. We used these data to determine the mean, minimum, and maximum body temperatures, as well as the variation in body temperatures displayed by focal *Eulamprus* in each treatment.

We also compared temperature selection of the focal *Eulamprus* by observing them in their individual enclosures in the laboratory, and recording whether they were sitting at the hot end of the enclosure over the heating tape, or elsewhere in the enclosure. Only active female *Eulamprus* were used for these observations, because the location of animals that were sheltering could not be determined. All observations were conducted between 10:00 and 11:00 hours. Each focal *Eulamprus* was observed on three consecutive days, and these data were used to calculate the average percentage of days that the individual was observed at the hot end of the enclosure.

Agonistic interactions might also affect food intake. Thus, we conducted a feeding trial on a subset of females ( $n = 10$ , randomly selected from each treatment) by observing the animals after introducing four crickets per lizard into the outdoor enclosure (as per the usual feeding regime). The crickets were randomly scattered throughout each enclosure. We observed the lizards through a small hole in the shade cloth, and recorded the number of crickets eaten by each individual.

Finally, we estimated the activity of focal *Eulamprus* by observing females in their individual enclosures in the laboratory, between 10:00 and 11:00 hours, and recording whether they had emerged, were active, or were under shelter. Each female was observed on three consecutive days, and these data were used to calculate the average percentage of days that she was sheltering when checked.

#### Physiology

Agonistic interactions may influence maternal physiology due to aggression-induced changes in behavior, or due to some aspect of the aggressive interaction itself. We measured levels of plasma corticosterone (a

stress hormone), maternal condition, sprint speed, and reproductive output. Blood samples were taken from focal *Eulamprus* five weeks after being housed in the outdoor enclosures (approximately mid-pregnancy) for analysis of plasma corticosterone levels. Blood samples were taken from all focal *Eulamprus*, including nine nonpregnant females (five from the solitary treatment, one that was housed with another *Eulamprus*, and three that were housed with *Egernia*) to test for any effect of pregnancy on corticosterone levels. Samples were collected from the postorbital sinus using a 75- $\mu$ L heparinized capillary tube. To minimize diel variations in corticosterone concentrations, all blood samples were taken between 09:00 and 14:00 hours, during the animals' normal activity period (Moore et al. 1991), and lizards within the three treatments were evenly sampled over this time period. However, we also recorded the time of day when each blood sample was obtained, and these times have been included as a covariate in analyses of the data.

To clarify whether or not this species responds to stress with increased corticosterone levels, and to determine what levels are produced by acute stress, we housed 24 female *Eulamprus* individually in plastic containers, as previously described, and allowed them 10 days to acclimate to their surroundings. These lizards were randomly allocated to either stress or control treatment groups ( $n = 12$  females in each). On the day of sampling, the room temperature was increased to 30°C to match the temperature at which blood from the focal *Eulamprus* in the outdoor enclosures was sampled. Individuals assigned to the stress treatment were all transferred to a single plastic container (60 × 30 × 20 cm, length × width × height), and were handled and chased around the container for 1 hour. The control group remained undisturbed in their home enclosures until immediately before sampling. Blood sampling was alternated between individuals from the stress and control groups, and all samples were taken between 12:00 and 13:30 hours, during the lizards' normal activity period.

Except for the stress treatment group (which was handled for an hour), all animals were caught within 1 minute of first disturbing them, and had a total handling time (from disturbance to completion of blood sampling) of <210 seconds. Handling time and time of day were included as a covariate in analyses of these data. Samples were stored on ice in heparinized tubes for 2–6 hours before centrifugation, and the plasma was stored at –80°C until assayed. Corticosterone was measured by radioimmunoassay (see Appendix A).

All focal female *Eulamprus* were measured for snout–vent length and mass at several times during the study: at capture, prepartum (when they were brought into the lab), immediately postpartum, and just before release. We used these data to determine if there was any effect of treatment on maternal condition at these times.

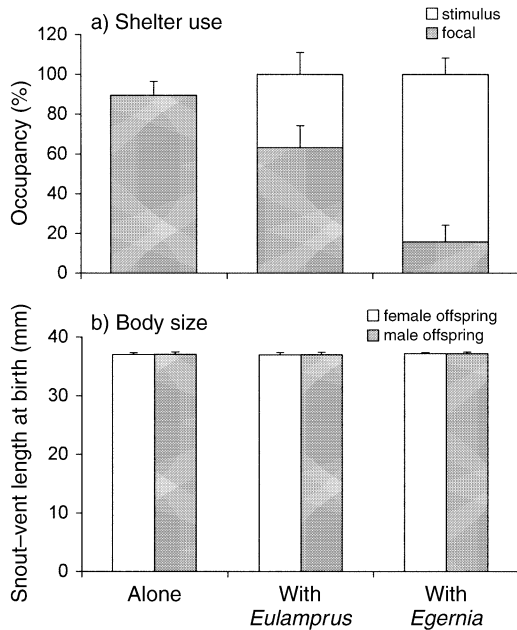


FIG. 1. (a) The percentage occupancy of the high-quality (brick) shelter sites by focal *Eulamprus heatwolei* within each treatment: when housed alone, with another female *Eulamprus heatwolei*, and with a female *Egernia saxatilis*. The histograms also show shelter-site use by stimulus *Eulamprus heatwolei* and *Egernia saxatilis* within the respective treatments. (b) Average snout-vent length of male and female neonates from focal *Eulamprus heatwolei* within each treatment. Values are means  $\pm$  SE.

We measured maximal maternal sprint speed four days postpartum on an electronically monitored raceway. All individuals were fed immediately postpartum, and subsequently fasted for the three days prior to sprinting. Each individual was raced four times down a 1-m track, and the fastest time over 0.25 m was used as the maximal sprint speed. Data from individuals obviously performing at less than their maximal capacity were excluded from analyses (Losos et al. 2002).

#### Reproductive output

We recorded the date when each female gave birth, as well as her litter size, total litter mass, and sex ratio of her offspring for comparison between treatments.

#### Offspring characteristics

We measured several behavioral and morphological characteristics of neonates from the focal *Eulamprus*. Specifically, we measured their size at birth, sprint speed, activity levels, selected temperature, food intake, and growth rates.

At birth, we sexed neonates and measured their snout-vent length, mass, and tail length. Sprint speed, activity, and selected temperature were measured as for their mothers. Neonates were remeasured for snout-vent length and mass just prior to release into the field (at 7–10 days of age), so that we could calculate their

growth rates. We quantified food intake of a subset of litters ( $n = 8$  litters from each treatment) immediately after racing. These neonates were transferred to individual plastic containers (115 mm diameter  $\times$  100 mm high), and were allowed 10 minutes to acclimate to their surroundings. We then introduced three small crickets into each container and recorded the number of crickets that had been eaten by each neonate after 30 seconds, and again after 10 minutes.

#### Statistical analyses

Data were analyzed using Statview 5.0 (SAS Institute 1998) and SuperANOVA 1.11 (Abacus Concepts 1991). Counts of *Eulamprus* occupying the brick shelter sites within each treatment were compared using chi-squared tests. Data on activity levels and temperature selection of focal *Eulamprus* and their neonates were square-root (arcsine) transformed, and all other data were  $\ln(x + 1)$ -transformed to fit the assumptions of parametric tests. Data for male and female neonates were averaged within each sex within each clutch, and were analyzed using repeated-measures ANOVA, with neonatal sex within litter as the repeated measure. Bonferroni corrections were applied where necessary.

## RESULTS

### Behavior

1. *Does the presence of an aggressive neighbor affect maternal shelter-site use?*—The high-quality (brick) shelter site was strongly preferred (occupied in 93% of cases overall, vs. 43% for the wooden shelter, 2% for the shade-cloth shelter, and 2% plastic shelter;  $\chi^2_3 = 150.18$ ,  $P < 0.0001$ ). However, fewer focal *Eulamprus* occupied the brick shelter when an *Egernia* was present than when the *Eulamprus* was alone ( $\chi^2_1 = 17.84$ ,  $P < 0.0001$ ) or was housed with a conspecific ( $\chi^2_1 = 8.95$ ,  $P = 0.01$ ; comparing all three treatments,  $\chi^2_2 = 22.75$ ,  $P < 0.0001$ ; Fig. 1a). The use of the brick shelter site by focal *Eulamprus* did not differ significantly when they were alone in an enclosure vs. housed with another *Eulamprus* ( $\chi^2_1 = 1.02$ ,  $P = 0.31$ ).

2. *Does the presence of an aggressive neighbor affect maternal body temperatures?*—Surprisingly, focal *Eulamprus* from all three treatments exhibited similar body temperatures (one-factor MANOVA with treatment as the factor, and the mean, minimum, maximum, and variation in body temperatures of focal *Eulamprus* as the dependent variables; Pillai's trace test [see Zar 1999],  $F_{8,36} = 1.76$ ,  $P = 0.12$ ; Appendix B). ANOVA tests revealed no significant treatment effects on any of the individual variables (see Appendix C).

3. *Does the presence of an aggressive neighbor affect maternal selected temperature?*—The percentage of active female *Eulamprus* that were observed at the hot end of their laboratory enclosures did not differ significantly among treatments (one-factor ANOVA with treatment as the factor;  $F_{2,44} = 1.21$ ,  $P = 0.31$ ).

4. *Does the presence of an aggressive neighbor affect maternal food intake?*—The number of crickets eaten by focal *Eulamprus* did not differ significantly among treatments (one-factor ANOVA with treatment as the factor;  $F_{2,36} = 1.99$ ,  $P = 0.15$ ).

5. *Does the presence of an aggressive neighbor affect maternal activity?*—To determine whether treatment affected maternal sheltering behavior, we compared the number of times that lizards were observed hidden vs. in the open when housed individually in the laboratory. Focal *Eulamprus* from each treatment did not significantly differ in the frequency with which they were observed under shelter (one-factor ANOVA with treatment as the factor;  $F_{2,43} = 0.34$ ,  $P = 0.71$ ).

#### Physiology

1. *Do Eulamprus exhibit increased plasma corticosterone levels in response to acute stress?*—Female *Eulamprus* that were exposed to acute handling stress had higher plasma corticosterone levels ( $206.88 \pm 11.33$  ng/mL; mean  $\pm$  SE) than did undisturbed females ( $16.95 \pm 1.81$  ng/mL). One-factor ANCOVA, with stress treatment as the factor, plasma corticosterone level as the dependent variable, and handling time and time of day as covariates, had the following results: for the stress treatment,  $F_{1,21} = 415.07$ ,  $P < 0.0001$ ; for handling time,  $F_{1,21} = 0.16$ ,  $P = 0.69$ ; for time of day,  $F_{1,21} = 0.07$ ,  $P = 0.79$ ; for all interactions,  $P > 0.05$ .

2. *Does pregnancy affect maternal stress levels?*—Pregnant and nonpregnant females did not differ significantly with respect to plasma corticosterone levels. Two-factor ANCOVA, with pregnancy status and treatment as the factors, plasma corticosterone level as the dependent variable, and handling time and time of day as covariates, had the following results: for pregnancy status,  $F_{1,48} = 0.38$ ,  $P = 0.54$ ; for treatment,  $F_{2,48} = 0.99$ ,  $P = 0.38$ ; for pregnancy status  $\times$  treatment interaction,  $F_{2,48} = 0.80$ ,  $P = 0.46$ ; for handling time,  $F_{1,48} = 1.34$ ,  $P = 0.25$ ; for time of day,  $F_{1,48} = 2.96$ ,  $P = 0.09$  (Appendix D). All interactions involving the covariates were nonsignificant.

3. *Does the presence of an aggressive neighbor affect maternal stress levels?*—Corticosterone levels did not differ significantly among focal *Eulamprus* from the three treatments. One-factor ANCOVA, with treatment as the factor, plasma corticosterone level as the dependent variable, and handling time and time of day as covariates, had the following results: for treatment,  $F_{2,43} = 0.14$ ,  $P = 0.87$ ; for handling time,  $F_{1,43} = 1.14$ ,  $P = 0.29$ ; for time of day,  $F_{1,43} = 1.87$ ,  $P = 0.18$  (Appendix D). All interactions involving the covariates were nonsignificant.

4. *Does the presence of an aggressive neighbor affect maternal body condition?*—The condition of the focal *Eulamprus* at capture, prepartum, immediately postpartum, and upon release did not differ significantly among treatments. Individual ANOVA/ANCO-

VA tests revealed no significant effect of treatment (Appendix C).

5. *Does the presence of an aggressive neighbor affect maternal sprint speed?*—The maximal sprint speed of focal *Eulamprus* was not significantly affected by treatment (one-factor ANOVA with treatment as the factor and maximum sprint speed as the dependent variable:  $F_{2,44} = 0.26$ ,  $P = 0.78$ ).

#### Reproductive output

1. *Does the presence of an aggressive neighbor affect maternal reproductive output?*—The reproductive output of female *Eulamprus* was not significantly affected by treatment. One-factor MANCOVA with treatment as the factor, litter mass, litter size, sex ratio of offspring, and date of birth as the dependent variables, and mothers' snout-vent length (SVL) as the covariate showed the following: for treatment,  $F_{8,82} = 0.63$ ,  $P = 0.75$ ; for SVL,  $F_{4,40} = 2.22$ ,  $P = 0.08$ . The interaction between these factors was nonsignificant (Appendix E). Further ANOVA tests revealed no significant effect of treatment on individual variables (see Appendix C).

#### Offspring characteristics

1. *Does the presence of an aggressive neighbor affect neonate characteristics?*—Our analyses detected no significant effects of treatment (or sex) on neonatal size and shape at birth (snout-vent length [Fig. 1b] condition, and relative tail length), sprint speed (Appendix F), sheltering behavior, selected temperature, feeding behavior, or growth rates (snout-vent length and mass; individual two-factor repeated-measures ANOVAs paired for neonatal sex within mother revealed no significant effect of treatment or sex; see Appendix G).

#### DISCUSSION

Our experiments provide no evidence that interspecific agonistic interactions affect fitness. The outdoor arenas in which we conducted our study incorporated many aspects of the complexity of the field. The enclosures were relatively large ( $2 \times 2$  m), contained a range of shelter sites offering different thermal regimes, and exposed the lizards to densities of conspecifics or heterospecifics similar to those they would encounter in the field. Nonetheless, enclosures can never exactly replicate the field, and aspects of the experimental situation therefore may have affected the outcome of our study. On one hand, our enclosures may have exaggerated the impact of aggressive interactions because the subordinate lizards were restricted to a 2-m<sup>2</sup> area, and therefore could not move completely out of the range of the *Egernia*, increasing the likelihood of aggressive interactions. On the other hand, our enclosures excluded predators and we provided sufficient food, aspects which, in the field, may actually provide key advantages of occupying the warmer shelter site. All that we can conclude is that, in a semi-

natural situation, intense agonistic interactions (sufficient to exclude the subordinate animal from the warmer shelter site) nonetheless had no discernible impact on a wide range of fitness-associated traits of the subordinate lizard.

The behaviorally mediated exclusion from shelter sites seen previously in the laboratory and the field was evident in the field enclosures, and we observed frequent aggressive encounters between enclosure mates. Our study also focused on a subset of the population likely to be most vulnerable to competitive effects: pregnant females. Because reproductive females of this and other species actively select high stable body temperatures, and offspring phenotypes are highly sensitive to such regimes (Schwarzkopf and Shine 1991, Shine and Harlow 1993), the design of our study provided a robust opportunity to detect any ecologically significant consequences of agonistic interactions. In view of this situation, our major result—that no such effects can be demonstrated—is deeply surprising (at least to us).

Despite intense aggressive interactions between these species, whereby female *Eulamprus* were (aggressively) excluded from otherwise preferred warmer shelter sites by *Egernia* (Fig. 1a), these interactions had no detectable effects on the behavior or physiology of the focal *Eulamprus*, nor on their reproductive output, nor on the phenotypic traits of their offspring. This result is not an artifact of low statistical power, because sample sizes were high enough, and variances in relevant traits low enough, that we would have detected biologically significant effects. In addition, power analyses on the 10 single-variable tests reported in this manuscript whose *P* values fell between 0.05 and 0.20 (the range within which power tests are useful: Peterman 1990) revealed that the power of these tests ranged from 0.31 to 0.53. Thus, despite a wide range of traits measured both for adult *Eulamprus* females and their offspring, our data provide no hint of any ecological “costs” to a subordinate individual (Appendices C and G).

The strong behavioral interference seen in our arena trials, whereby female *Eulamprus* were excluded from higher quality (hotter) shelter sites by aggressive *Egernia*, fits well with results from our previous trials, both in the laboratory and the field (Langkilde and Shine 2004). Based on such aggressive exclusion, we predicted that female *Eulamprus* would experience lower body temperatures, would have reduced access to food, and hence would show significant decreases in their own body condition and locomotor performance, as well as higher stress levels; and that these “costs” in turn would translate into viability decrements for their offspring. In these predictions, we were comprehensively wrong.

Although female *Eulamprus* were excluded from thermally optimal shelter sites by *Egernia*, they were able to maintain “normal” body temperatures, presum-

ably by basking opportunistically at times and in places where attack from the resident *Egernia* was less likely. However, such avoidance may be costly in the field, where basking in the open to compensate for a thermally suboptimal shelter site may increase an animal’s vulnerability to predation. In keeping with this scenario, we observed *Eulamprus* to cease basking and flee as soon as an *Egernia* emerged from shelter and approached them. Similarly, the presence of a larger and more aggressive lizard did not significantly reduce food intake by the *Eulamprus*; instead, they fled as soon as they seized a cricket, and thus were able to consume the prey item without it being commandeered by *Egernia* (which happened if the *Eulamprus* remained within the larger lizard’s field of view; T. Langkilde, *personal observation*).

Perhaps reflecting the possibility that *Eulamprus* are able to modify their behavior in order to minimize the thermal and nutritional costs of aggression by *Egernia*, corticosterone levels of our focal lizards were not increased by the aggressor’s presence. Our validation trials showed that *Eulamprus* do express increased corticosterone levels in response to acute (handling) stress, and do not suppress their stress response during pregnancy (unlike some reptiles and mammals; Neumann et al. 1998, Hamann et al. 2003). The corticosterone levels that we measured in *Eulamprus* are at the high end of the range of values reported for other species, but are not unusual (Meylan et al. 2002, Comendant et al. 2003, Jones and Bell 2004). The simplest explanation for the observed lack of effect on corticosterone levels is that *Eulamprus* were not stressed by the presence of an aggressive *Egernia*. However, it would be interesting to explore the level of corticosterone in response to stress in these animals exposed to interspecific aggression. Elevated stress levels over long periods (weeks to months) can have negative consequences, including reproductive suppression (Sapolsky 1992), reduced immuno-competence (Munck et al. 1994), and lower insulin production (Bremner 1999). Therefore, animals may reduce their baseline corticosterone levels in response to long-term exposure to stress, but respond more intensely to subsequent acute stress (Romero 2004). In support of this possibility, our preliminary data on *Eulamprus* show that time in captivity affects corticosterone levels in response to handling stress, but does not affect baseline corticosterone levels (T. Langkilde and R. Shine, *unpublished data*).

Despite abundant evidence that a mother’s thermal regimes and stress levels can influence the phenotypic traits of her offspring in viviparous lizards (Wapstra 2000, Cree et al. 2003), as well as a variety of other taxa (including mammals and birds; Hennessy et al. 1999, Lay and Wilson 2002), we found no effects of aggression on the morphology or locomotor performance of the offspring produced by our focal females. At least part of this lack of effect is due to the fact that

female *Eulamprus* were able to maintain relatively high body temperatures overall, despite being restricted to cooler, less-than-optimal shelter sites at night. Nocturnal temperatures may generally fall below the minimum for embryonic development, even in shelter sites that attain high temperatures during the day; thus, thermal regimes at this time may have little effect on embryogenesis (Georges 1989, Andrews et al. 1997). Critically, the pregnant female *Eulamprus* were able to maintain high constant temperatures during daylight hours, possibly by avoiding the aggressive *Egernia*. Because any diurnal thermal differentials between females in the various treatments were minimal, any effects of incubation temperature on offspring traits also were vanishingly small.

So why do these lizards fight in such a predictable, repeatable fashion over shelter sites that appear to confer no benefit to the resident? As previously noted, the lack of predation pressure and the provision of food in our outdoor enclosures may have masked potential advantages of occupying the warm shelter. The higher body temperatures available to lizards using warmer shelter sites may permit faster movement within the retreat site, thereby facilitating escape from predators (such as snakes; Shine 1977, O'Connor 2004) that penetrate the retreat. Higher temperatures within the retreat site also may permit earlier onset of feeding in the morning, or earlier initiation of reproductive activity on a seasonal basis. Alternatively, there may be spatial or temporal variation in the benefits of securing a warm shelter site, such that these benefits apply only under certain conditions (different from those imposed during our study). For example, an increased body temperature may be beneficial only on cold days, during an unusually cold season, or in cold geographic locations; and during very wet times of year, occupying a warm shelter may reduce the risk of fungal infection (common in *Egernia*; T. Langkilde and R. Shine, *personal observation*). Finally, shelter-site utilization and defense behaviors may result from prior episodes of selection during the phylogenetic history of these taxa, and thus may have no current fitness benefits. Further studies examining a range of potential ecological benefits at various spatial and temporal scales are needed to gain a full understanding of the benefits of retreat-site exclusion behaviors in this montane lizard assemblage.

In our study, the focal *Eulamprus* were able to minimize or eliminate the potentially serious ecological consequences of interspecific aggression, presumably by modifying their behavior in flexible ways. Such impact minimization might be widespread in lizards, or might be an evolved trait specific to the interaction between these two taxa, reflecting long periods of coevolutionary adjustment between them in areas of sympatry in southeastern Australia. To tease apart these two possibilities, we need further research on a range of study systems that differ in the degree of sympatry of the component species. Strong effects of agonistic

interactions from invasive species (Williamson 1996, Low 1999) hint at the possibility that coevolutionary adjustments can minimize the costs of such interactions, but more data are needed.

Our study also provides a cautionary tale about the difficulty of extrapolating observations of agonistic interactions per se (i.e., direct behavioral interactions, resulting in effects such as shelter-site exclusion) to the conclusion that such interactions will have a significant ecological impact on the species involved. When laboratory manipulations or field observations reveal intense levels of agonistic interactions and aggressive exclusion, it is tempting to assume that the "losers" of such interactions inevitably will experience biologically significant ecological costs. However, our study provides strong evidence that, at least in a field-enclosure situation, the "losers" were able to continue functioning normally, with no evidence of any overt decrements in fitness-related traits of themselves or their progeny. Therefore, even when two species (or individuals within a species) interact aggressively and exclude each other from preferred habitats, the competitive effects of such interactions may be trivial or nonexistent.

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#### APPENDIX A

Methods for measuring plasma corticosterone levels are available in ESA's Electronic Data Archive: *Ecological Archives* E086-090-A1.

#### APPENDIX B

A figure presenting the effect of the presence of an aggressive neighbor on maternal body temperatures is available in ESA's Electronic Data Archive: *Ecological Archives* E086-090-A2.

#### APPENDIX C

A table presenting ANOVAs for the effect of treatment on maternal characteristics of *Eulamprus heatwolei* is available in ESA's Electronic Data Archive: *Ecological Archives* E086-090-A3.

#### APPENDIX D

A figure presenting the effect of the presence of an aggressive neighbor on maternal stress levels is available in ESA's Electronic Data Archive: *Ecological Archives* E086-090-A4.

#### APPENDIX E

A figure presenting the effect of the presence of an aggressive neighbor on maternal reproductive output is available in ESA's Electronic Data Archive: *Ecological Archives* E086-090-A5.

#### APPENDIX F

A figure presenting the effect of the presence of an aggressive neighbor on neonatal sprint speed is available in ESA's Electronic Data Archive: *Ecological Archives* E086-090-A6.

#### APPENDIX G

A table presenting ANOVAs for the effect of treatment on offspring characteristics is available in ESA's Electronic Data Archive: *Ecological Archives* E086-090-A7.